



High-resolution biochronology and diversity dynamics of the Early Triassic ammonoid recovery: The Dienerian faunas of the Northern Indian Margin



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ABSTRACT

A new high resolution biozonation based on the Unitary Association (UA) method is constructed for the Dienerian ammonoid succession of the Northern Indian Margin. It includes 12 UA-zones and leads to the subdivision of the Dienerian into three parts (early, middle and late). The corresponding diversity analyses, coupled with results previously obtained for the early Smithian ammonoids of the same regions, highlight the four following phases: (1) a first modest peak of diversity in the early Dienerian; (2) a very low diversity persisting throughout the middle Dienerian; (3) a slow increase of diversity during the late Dienerian, and (4) a marked diversification in the early Smithian. Turnover rates are very high during this entire time interval, and the boundaries between early–middle and middle–late Dienerian are emphasised by complete renewals of the ammonoid faunas. The low diversity values in the middle and early late Dienerian are concomitant with an anoxic event on outer continental shelves and coincide with warmer temperatures than those of the early Dienerian and early Smithian. This diversity pattern stands in strong contrast with the credo of a protracted or stepwise recovery following the end-Permian mass extinction. Together with the end-Smithian extinction, the middle and early late Dienerian diversity crises were likely both radical setbacks in the recovery of Early Triassic ammonoids. However, these two diversity crises do not necessarily imply identical environmental triggers that ultimately led to anoxic bottom waters on outer continental platforms in both cases.

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1. Introduction

Modes and rates of biotic recovery following the end-Permian mass extinction are currently attracting a lot of efforts. Ammonoids have been documented to be one of the fastest clades to recover and even to largely overshoot their previous Permian record highs (Brayard et al., 2009). At the genus level, ammonoids show a low diversity in the Griesbachian, a slight increase during the Dienerian and an explosive radiation in the early Smithian (Brayard et al., 2006, 2009). Such a pattern provides the general outline of diversity trends, but is also influenced by uneven taxonomical practices across authors, relatively coarse time bins and the absence of consensus about some stage and sub-stage boundaries (i.e. Induan–Olenekian ill defined boundary; Brühwiler et al., 2010a). More recently, a significant advance toward a refined diversity analysis (Brühwiler et al., 2010b) hinged on a new, highly resolved biozonation of the Smithian from the Northern Indian Margin (NIM).

The NIM has long been recognised as a key area for the establishment of the Early Triassic time scale (Jenks et al., 2015). The Salt Range

(Pakistan) and Spiti District (Northern India; Fig. 1) are especially notorious for their abundant and well preserved ammonoid faunas since the pioneer works of Waagen (1895) in the Salt Range and of Diener (1897) and Krafft and Diener (1909) in Spiti. However, until recently, no thorough and modern revisions of the taxonomy and biostratigraphy of the ammonoids of these two regions have been published. The understanding of most taxa described in these pioneering works is hampered by the small sample sizes and their approximate stratigraphic positions. Following the revision of the Smithian ammonoids from the Salt Range (Brühwiler et al., 2012a) and Spiti district (Brühwiler et al., 2012b), new abundant and well-preserved material allowed us to thoroughly revise the taxonomy and biostratigraphy of the Dienerian ammonoids from these two basins (Ware et al., submitted-a, submitted-b). As for the Smithian, they represent the most complete and detailed Dienerian ammonoid records known worldwide, with 12 Dienerian local maximal horizons in the Salt Range and 10 in Spiti, compared to only four horizons in Canada (Tozer, 1994), three in South Primorye (Shigeta et al., 2009) and four in Siberia (Dagys and Ermakova, 1996).

Here we present a new high-resolution ammonoid zonation for the Dienerian of the NIM based on a synthetic biochronological analysis of the Salt Range and Spiti basins at the species level. This new biostratigraphic scheme is based on bed by bed extensive collections in order

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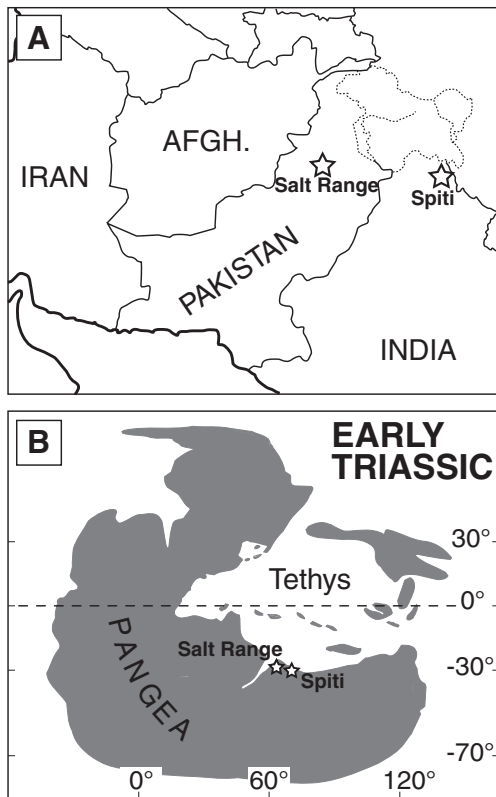


Fig. 1. [A] Situation of the Salt Range and Spiti; [B] simplified early Triassic palaeogeography (modified after Brayard et al., 2006) with the position of the Salt Range and Spiti.

to produce a reliable taxonomy reflecting intraspecific variation as well as the best possible resolution in time. Correlation of the Dienerian ammonoid succession of the NIM with other regions will need additional, similarly detailed work. Possible correlations are discussed in Ware et al. (submitted-a). This succession of the Dienerian provides a robust reference scheme for Dienerian times and further correlations at larger geographical scales. The hitherto poorly known Dienerian faunas can now contribute to an improved understanding of the Early Triassic recovery. The new highly resolved biostratigraphic framework allows the analysis of the biodiversity dynamics of the Dienerian ammonoids from the NIM with unprecedented detail, and to compare it with palaeoenvironmental proxies obtained from the same sections.

2. Material and methods

The method used here is the same as in Brühwiler et al. (2010b). Hence, only a short description is provided. The reader is referred to Brühwiler et al. (2010b) for further details. The new Dienerian biostratigraphic framework and ammonoid diversity data can thus be directly compared to the Smithian ones of Brühwiler et al. (2010b, updated according to Brühwiler et al., 2012a and the new classification established in Ware et al., submitted-a), thus significantly expanding downward the available high-resolution time window within the Early Triassic of the NIM.

2.1. Taxonomic data sets

In the Salt Range, Dienerian ammonoids were collected from four areas (Nammal, Chiddru, Amb and Wargal). Several sections were sampled in these four areas, and a composite section was constructed for each of them based on bed-by-bed correlations, an approach recommended by Guex (1991) for enhancing the completeness of the stratigraphic ranges of species. In Spiti, Dienerian ammonoids were

collected from eight sections distributed in three areas (Mud, Guling and Lalung). Details concerning the localities, the stratigraphy and ammonoid taxonomy are given in Ware et al. (submitted-a) for the Salt Range and in Ware et al. (submitted-b) for Spiti.

The first step consists in a detailed revision and standardisation of the ammonoid taxonomy, with special emphasis on intraspecific and ontogenetic variation. The results of this revision are presented in Ware et al. (submitted-a, submitted-b). This led to an improved understanding of the taxonomy of Dienerian ammonoids, inclusive of above the specific level, where many genera were so far poorly defined. A grand total of 47 species were recognised. For the biochronological analysis, occurrences based on poorly preserved material or based on rare taxa found in only a single sample were removed from the initial dataset. For the Dienerian, five such species with unique occurrences were omitted and then re-inserted in the dataset after completion of the biozonation.

2.2. Unitary Association method

The biozonation presented here is based on the Unitary Associations (UA) method of Guex (1991). A general account of the advantages of this method is given in Brühwiler et al. (2010b), and for the exhaustive description of the UA method the reader is referred to Guex (1991), Monnet and Bucher (2002) and Monnet et al. (2015). The UA analysis was performed with the palaeontological data analysis software PAST (Hammer et al., 2001). This method has several crucial advantages. First, UAs are discrete (non-continuous) time bins consisting of unique and mutually exclusive assemblages of taxa, isolated from each other by intervals of separation, thus faithfully reflecting the discontinuous nature of the fossil record. These exclusive assemblages are maximal sets of co-occurring species and can accommodate any later modifications such as is the case for all approaches based on the fluctuating positions of First Occurrences and Last Occurrences. Second, Escarguel and Bucher (2004) demonstrated that such zones based on the maximal association principle provide reliable counts of species richness, whatever the unknown duration of each UA-zone.

The construction of UA-zones includes the following steps. First, an occurrence matrix for every section of the Salt Range and Spiti is built (Appendix A–Table 1). Then, the regional UAs for the Salt Range and Spiti are computed separately using PAST. The regional zonations and species occurrences obtained (Appendix A–Table 2) are thus treated as a two sections dataset, which is again processed with PAST to obtain UAs at the NIM palaeogeographical level. Taxa with a single occurrence that were initially removed from the dataset are then dated and re-inserted into the zonation. Finally, UAs having a poor lateral reproducibility and/or which are based on very rare characteristic species are merged to construct the UA-zones sequence for the NIM (see discussion in Section 4.1).

2.3. Diversity dynamics

Analyses of diversity dynamics follow the same procedure as Brühwiler et al. (2010b). Species richness corresponds to the number of species in a UA-zone, and originations and extinctions correspond to the number of species that appear and disappear between two successive zones. Origination rate is the number of originations divided by the species richness of the subsequent zone; extinction rate is the number of extinctions divided by the species richness of the previous zone. The turnover is the sum of originations and extinctions, and the turnover rate is the turnover divided by the total species richness of the two corresponding successive zones. A rarefaction analysis on the species richness was conducted using PAST to estimate the bias induced by sample size on species counts. This potential sampling bias was further investigated with incidence-based total richness estimators calculated with Estimates (Colwell, 2009). An additional analysis at

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